A NEW APHID FROM THE CRETACEOUS OF BOTSWANA

by R. J. RAYNER *and* S. B. WATERS

ABSTRACT. The forewing of a fossil aphid *Siphonophoroides*? *orapaensis* (Homoptera: Aphididae) is described. It is the first fossil aphid from Africa. Although it is impossible to assign it with confidence to a distinct extant or extinct family of the Aphidoidea, it has been placed tentatively in the Drepanosiphidae. Its similarity with members of the genus *Siphonophoroides* had led to its tentative inclusion in this group. The fossil was discovered in middle Cretaceous sediments from the Orapa Diamond Mine, Botswana. The presence of an aphid has implications for a palaeoenvironmental analysis of this part of Africa in the Cretaceous; this aphid was a specialized parasite on early angiosperms and the Orapa climate was seasonal and temperate with spring and summer rains.

DESPITE their almost world-wide distribution, and some 4000 extant species, aphids are rather rare in the fossil record. This is presumably due both to their soft-bodied nature and small size. The unusual sedimentary conditions prevailing in the Orapa kimberlite crater during the Cretaceous (McKay and Rayner 1986; Rayner 1987), however, have preserved a large number of insect remains, and among them an aphid wing was recently discovered. The specimen is the first fossil aphid from Africa.

Geological setting. Mining operations at Orapa have exposed fossiliferous sediments overlying a large diamondiferous kimberlite (McKay and Rayner 1986). The sediments, a sequence of shales and mudstones, were laid down in a crater lake, and are therefore not connected to other Cretaceous sediments. The eruption of the kimberlite has been dated using U/Pb and fission track techniques at *c*. 95 million years. The nature of the sediments indicates that their deposition occurred almost immediately after the eruption (Rayner 1987; Waters 1989*a*, *b*).

Preservation. The wing is preserved as a compression fossil on a brown mudstone. The outline and venation are preserved as black lines on the sediment surface, which indicates that organic material remains.

Methods and material. The composite photograph was taken with a Zeiss SV8 photomicroscope using double polarized light, which enhanced the natural contrast (text-fig. 1). It was impossible to get all of the wing in focus in one frame due to vertical movement associated with drying and cracking of the sediment. A drawing was therefore made with the use of a *camera lucida* (text-fig. 2).

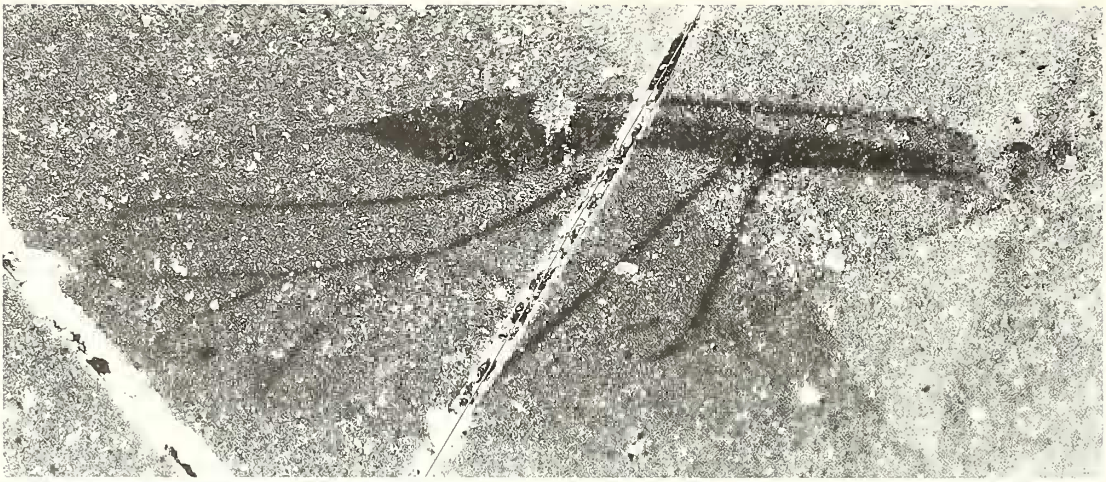
SYSTEMATIC PALAEONTOLOGY

Superfamily APHIDOIDEA Borner, 1930
Family ?DREPANOSIPHIDAE Herrich-Schaeffer (Shaposchnikov, 1979)
Genus ?SIPHONOPHOROIDES Buckton, 1883

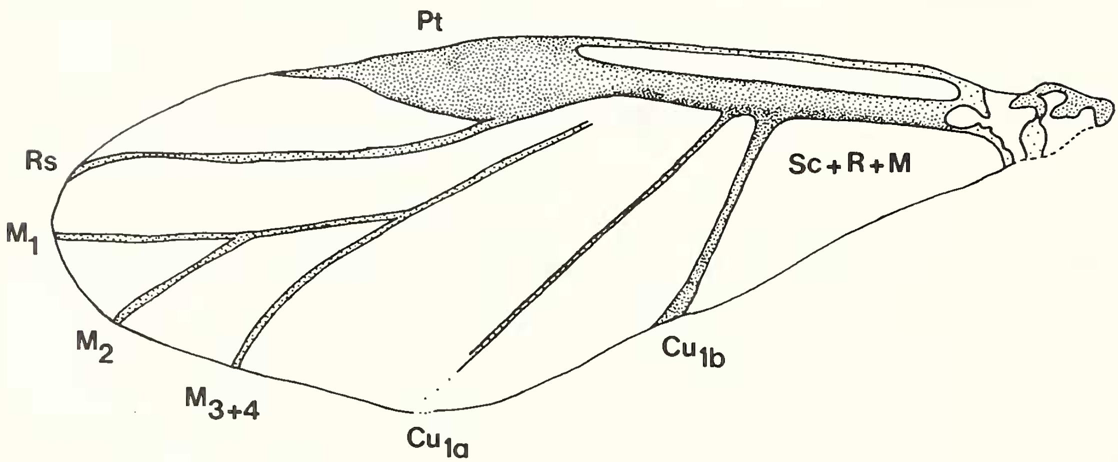
Siphonophoroides? *orapaensis* sp. nov.

Text-figs. 1 and 2

[Palaeontology, Vol. 32, Part 3, 1989, pp. 669–673.]



TEXT-FIG. 1. Forewing of *Siphonoroides*? *orapaensis* n. sp., Cretaceous of Orapa, Botswana. ×480.



TEXT-FIG. 2. *Camera lucida* drawing of the forewing of *Siphonoroides*? *orapaensis* n. sp. Pt, pterostigma; Rs, radial sector; M_1, M_2, M_{3+4}, posterior (sectoral) branches of media; Cu_{1a}, anterior branch of cubitus; Cu_{1b}, posterior branch of cubitus; Sc+R+M, subcostal+radial+medial trunk. ×480.

Holotype. The Bernard Price Institute for Palaeontological Research Palaeobotanical Herbarium, University of the Witwatersrand, Johannesburg, South Africa, No. BP/2/25970; single wing on brown mudstone, from Orapa, Botswana.

Derivation of name. Latinized form of Orapa, the site of discovery.

Diagnosis. Wing narrow, elongate, 3·25 mm long by 1·15 mm at the broadest point; anterior margin slightly concave apically; separate cubital branches Cu_{1a} and Cu_{1b} present with their bases not widely separated at 0·14 mm; Cu_{1a} and Cu_{1b} simple, less than half the length of the forewing, 1·3 and 0·7 mm respectively; Cu_{1b} and Sc+R+M trunk strongly pigmented, more so than other veins; M with two forks, M_2 and M_{3+4}, of intermediate lengths which leave M at equal distances; M originating just proximal to base of pterostigma at an acute angle; Rs simple, relatively straight, 1·25 mm long, and originates from proximal part of pterostigma; all veins reach wing margin of the wing; pterostigma elongate and rather narrow.

Description. As for diagnosis.

DISCUSSION

The wing venation indicates that this specimen belongs to the aphids. Important diagnostic features are that only one prominent longitudinal vein is present, and the radial sector vein (Rs) is separate from the stigma. Assigning the specimen with certainty to a family of the Aphidoidea has proved difficult. The absence of morphological features additional to those of the wing is the major problem (Heie (1985) listed primitive and advanced features which are useful for confident classification). Another complication is that some Mesozoic aphids belong to diverse, strongly specialized groups (Shaposhnikov 1983), which are now extinct (Kononova 1976). Some little specialized aphids, belonging to groups containing the ancestors of more than one family, must also be expected to be found in Mesozoid deposits (Heie personal communication). Bearing these points in mind, the single fossil wing has tentatively been placed in the extant family Drepanosiphidae. Its similarity to an extant genus of this family: *Siphonophoroides* Buckton, 1883, is likewise acknowledged, by tentatively placing the specimen in this group, but, at the same time, it is stressed that members of this genus are considerably younger than the Orapa specimen and they have been found far from Africa. *Siphonophoroides* is represented by several Tertiary species in North America and northern Europe. Although only a few morphological characters are visible, the wing fossil is described as a new species *S*? *orapaensis*. There are dangers inherent in such a practice, but a fossil without a name can easily be forgotten. The specimen is, however, significant in that it is similar to some Tertiary aphids, but is much older and it is found in a different hemisphere. Also, most of the wing characters of *S*? *orapaensis* are plesiomorphic, and its overall appearance is primitive.

Most similarities of *S*? *orapaensis* with other groups are symplesiomorphies. There are four distinct plesiomorphies: a, the subcosta, radius, media and cubitus are united at the base to form a strong longitudinal main vein; b, the pterostigma is well-developed, rather elongate; c, the radial sector leaves the basal part of the pterostigma; d, the media has two forks, and one apomorphous character, which has evolved by convergence or parallelism in many aphid families; i.e. the branching of the cubitus inside the main vein thereby forming two separate branches, Cu_{1a} and Cu_{1b}.

Although overall morphology of the wing is primitive, it shows similarities with several aphids from the present as well as the geological past. The cubitus is strong and dark, as in the Cretaceous *Elektraphididae* Steffan, 1968 (Phylloxeroidea) and in *Triassoaphis* Evans, 1956. The origin and branching of M resembles that of *Jurocallis* Shaposhnikov, 1979 from the Jurassic. The long straight Rs, leaving the proximal half of the pterostigma, is found in *Siphonophoroides* Buckton, 1883 (Drepanosiphidae) from the Tertiary and *Oviparosiphum* Shaposhnikov, 1979 (Oviparosiphidae) from the Cretaceous and in Recent species of *Mindarus* Koch, 1857 (in Heie 1987). The origin of the cubital branches is as in *Oviparosiphum*, and the shape of the pterostigma is similar to *Siphonophoroides*. The greatest overall similarity of the aphid wing is to *Siphonophoroides* spp., however, and in the absence of further details, the specimen is considered to be a possible member of this genus.

The oldest fossil aphid, *Triassoaphis cubitus*, was described from Triassic sediments (Evans 1956). It is likely, however, that the first aphids evolved in the Carboniferous, or Permo-Carboniferous times, from the same stock that gave rise to the extinct Archescytinidae and other Homoptera, which are all thought to have parasitized gymnosperms (Heie 1967). Shaposhnikov (1979) described seven species of aphid from the Late Jurassic/Early Cretaceous, approximately the time of first appearance of the angiosperms; however, he suggested that gymnosperms were their hosts.

Heie (1985) suggested that the first true aphids were polyphagous and included plant sap in their diet; they did not have host alternation, but could probably feed on both gymnosperms and early (unknown) angiosperms; they were probably oviparous through all generations and only facultatively parthenogenetic.

In contrast to these early representatives, the hosts of most present-day aphids are angiosperms, although some live on gymnosperms and a few on ferns, *Equisetum*, and mosses (Dixon 1973). All homopterans are terrestrial and phytophagous (Jacobs 1985), and they are frequently found in large numbers on plants (Dixon 1985). Aphids may be encountered on young shoots, under leaves, on branches or on the roots of their hosts; some (which overwinter as eggs) have host alternation, which means that they utilize primary and secondary hosts as food sources (Millar 1985). The primary hosts are the plants (usually trees) on which the diapause eggs are laid.

Most species are polymorphic and have a complex life-cycle which may be correlated with sex, season, climate and habitat stability. In most Aphidoidea there are two kinds of parthenogenetic females, apterae and alatae. The apterous condition is associated with rapid growth and reproduction and the winged condition with dispersal and migration (Jacobs 1985).

Of the many predators of aphids, most are insects; they include the larvae and adults of lacewings and most ladybird beetles, the larvae of some hoverflies, cecidomyid larvae and some Hymenoptera. Certain birds also eat aphids, especially when these are abundant or when other food is scarce. Few aphids thrive in hot, dry weather; they favour well-watered ground which supports quantities of green and actively growing vegetation (Dixon 1985).

Whether present-day aphid life strategies, and the complex interactions with other insects and plants, were common features in the Cretaceous is unknown. We may, however, speculate that the association with angiosperms arose with their first appearance. Angiosperm and pteridophyte remains have been recovered from Orapa sediments, but, to date, no gymnosperms. Recent aphids, similar to *Siphonophoroides*, parasitize *Acer* and other angiosperm trees; although *Acer* is a northern genus, similar fossil leaves have been found at Orapa (Bamford personal communication). This invites the suggestion that *Siphonophoroides*? *orapaensis* used these plants as hosts. There are numerous predatory insect remains from Orapa: beetles, wasps, lacewings, and flies (Waters 1989*a*, *b*), as well as spiders, and, almost certainly, some were feeding on aphids. The presence of this insect reinforces the notion that the climate was seasonal and temperate with spring and summer rains, although some recent aphids occur in climates with uniform precipitation and temperature throughout the year.

Acknowledgements. We thank the Office of the President of Botswana, and Debswana mining company for permission to collect and work on the fossil material. We receive financial assistance from the University of the Witwatersrand, the CSIR, and The Friends of the Museum, Gaborone, all of whom are gratefully acknowledged. D. Pearce assisted with the photography. Special thanks are due to O. E. Heie who contributed much to this paper. This is an OHSG publication.

REFERENCES

BORNER, C. 1930. Beiträge zu einem neuen System der Blattlause. *Arch. klass. u. phyl. Ent.* **1**, 115–180.

BUCKTON, G. B. 1883. *Monograph of the British Aphides*, vol. IV: *Fossil aphids*, 144–178. London.

DIXON, A. F. G. 1973. *Studies in Biology no. 44. Biology of Aphids*, 58 pp. Edward Arnold, London.

—— 1985. *Aphid Ecology*, 157 pp. Blackie and Son, London.

EVANS, J. W. 1956. Palaeozoic and Mesozoic Hemiptera (Insecta). *Austr. J. Zool.* **4**, 165–258.

HEIE, O. E. 1967. Studies on fossil aphids (Homoptera: Aphidoidea), especially in the Copenhagen collection of fossils in Baltic amber. *Spolia Zool. Musei Hauniensis* **26**, 1–27.

—— 1981. Morphology and phylogeny of some Mesozoic aphids (Insecta, Hemiptera). *Ent. scand. Suppl.* **15**, 401–415.

—— 1985. Fossil aphids. A catalogue of fossil aphids, with comments on systematics and evolution. *Proceedings of the International Aphidological Symposium on Evolution and Biosystematics of Aphids in Jablonna*, 1981, 101–134. Polska Akademia Nauk, Warszawa.

—— 1987. Palaeontology and phylogeny. *In* MINKS, A. K. and HARREWIJN, P. (eds.). *Aphids. Their Biology, Natural Enemies and Control*, vol A, 367–391. Elsevier, Netherlands.

JACOBS, D. H. 1985. Order Hemiptera. *In* SCHOLTZ, C. H. and HOLM, E. (eds.). *Insects of Southern Africa*, 112–148. Butterworth, Durban.

KONONOVA, E. L. 1976. Extinct aphid families (Homoptera: Aphidinea) of the Late Cretaceous. *Palaeont. J.* **10**, 352–360.

MCKAY, I and RAYNER, R. J. 1986. Cretaceous fossil insects from Orapa, Botswana, *S. Afr. J. Ent.* **49**, 7–17.

MILLAR, I. 1985. Aphidoidea. *In* SCHOLTZ, C. H. and HOLM, E. (eds.). *Insects of Southern Africa*, 164–168. Butterworth, Durban.

RAYNER, R. J. 1987. March flies from an African Cretaceous springtime. *Lethaia* **20**, 123–127.

SHAPOSHNIKOV, G. CH. 1979. Late Jurassic and early cretaceous aphids. *Palaeont. J.* **4**, 66–78.

—— 1983. Evolution of morphological structures in aphids (Homoptera, Aphidinea) and habits of the recent and Mesozoic representatives of the group. *Revue d'Entomologie de l'USSR* **59**, 39–59.

STEFFAN, A. W. 1968. Elektraphididae, Aphidonorum nova familia e succino baltico (Insecta: Homoptera: Phylloxeroidea). *Zool. Jb.* (Syst.), *Mainz*, **95**, 1–15.

WATERS, S. B. 1989*a*. A new hybotine dipteran from the Cretaceous of Botswana. *Palaeontology*, **32**, 657–667.

—— 1989*b*. A Cretaceous dance fly (Diptera: Empididae) from Botswana. *Syst. Ent.* **14**, 233–241.

R. J. RAYNER and S. B. WATERS

Bernard Price Institute for Paleontological Research
University of the Witwatersrand
WITS 2050
South Africa

Typescript received 24 November 1987
Revised typescript received 20 August 1988